Marine Research

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Marine Research
1958 No. 6

Herring (*Clupea harengus* L.) in Aquaria

II. Feeding

By J. H. S. BLAXTER, M.A. and F. G. T. HOLLIDAY, B.Sc.

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Herring (*Clupea harengus* L.) in Aquaria

II. Feeding

INTRODUCTION

e food and feeding habits of herring caught at sea have been studied, for instance, by Pearcy Hardy (1924), Jespersen (1924), Ogilvie (1934) and Savage (1931, 1937). In particular, Jespersen Mužinić (1931) and Savage (1937) considered the question of times of feeding and rates of on. This and related problems have been studied in herring kept in aquaria by Battle *et al* (1936), (1938), Johnson (1939), Bückmann, Harder and Hempel (1953), Verheijen (1953), Schäfer (1955) Scattergood and Sindermann (1957). Digestion in herring has been studied by Almy (1926) and (1935). In addition daily feeding cycles at sea of *Sardina pilchardus* have been studied by Vućetič and feeding of *Sardinops caerulea* in aquaria by Anon (1952) and Loukashkin and Groody (1955). jen (1956) also kept *Clupea pilchardus* in aquaria.

other study of feeding of herring in aquaria is recorded here. It was carried out partly to obtain lata needed for further experimental work on herring, and partly to obtain data which might be o help explain the behaviour of herring in the sea.

METHODS

periments were started in 1952 but most of the work was carried out during 1957. The herring, immature two-year-old fish, ranging from 16-22 cm in length, were caught at the mouth of the Dee by beach seine. They were transferred in carboys or bins to a large concrete tank measuring .8 × 1.1 metres containing sea water of salinity 30‰. The tank was covered by a ridged roof with trap doors on the east side. A limited amount of light entered through the open ends.

e temperature of the water was maintained at a minimum of 11°C during most of the experiments; asions during the summer it rose to 16°C. The volume of water was great enough to prevent rapid tions of temperature. The water was continuously aerated and circulated through a filter bed of nd gravel. Further details of the tanks and factors involved in establishing herring are described rish, Blaxter and Holliday (1958).

RESULTS

TION OF FEEDING

e of the difficulties in establishing herring in aquaria is to induce the fish to feed. In these experi- feeding usually commenced within 7 to 14 days after capture. The following different types of ere tried and a preference found:—

Chopped squid (*Loligo*) Chopped mussel (*Mytilus*) Chopped limpet (*Patella*)	Used with most success.
Chopped earthworm (*Lumbricus*) Chopped herring muscle Fish roe (cod, plaice, herring) Liver (beef)	Used with less success.

Live brine shrimps (*Artemia salina*) Live *Gammarus* Live *Calanus* Dried *Calanus* Fish meal Bread Egg white Commercial fish food ("Hykro" flakes, "Spratts", Ants' eggs)	Used without success.

Prior to 1957 the herring were maintained on chopped mussel. During 1957 they were fed ma on chopped squid with occasional feeds of chopped limpet or mussel.

A distinct preference for certain types of food has also been shown in other fish. Lovern (19 working on the eel (*Anguilla vulgaris*), showed that they preferred earthworms, mussels and herring f in that order. Eels could not, in fact, be induced to commence feeding on herring flesh even if sta for five months and would only take it after eating other food first. Stephenson and Grant (1957) fo a definite preference in the callop (*Plectroplites ambiguus*). This knowledge was of value in enabling t workers to feed the fish with food which was regularly obtainable and highest on the "palatability"

Herring normally feed on crustaceous food, notably *Calanus* and euphausiids and on *Limacina*, *Sag Oikopleura* and small fish such as *Ammodytes* (Hardy, 1924, etc.). In aquaria various foods have been u such as chopped *Mytilus* and *Mya*, *Mysis*, *Gammarus*, *Homarus* larvae, *Hyperia*, *Calanus* and *Meganyctiph* by Battle *et al* (1936), chopped *Meganyctiphanes* and *Calanus* by Johnson (1939), beef, *Daphnia*, *Enchyt* and *Calliphora* larvae by Verheijen (1953), copepods and *Daphnia* by Bückmann *et al* (1953) and gre sea mussel by Farrin *et al* (1957).

The appetite preference found in our experiments is given above. Without doubt the herring prefe chopped squid, *Loligo*, chopped mussel, *Mytilus* and chopped limpet, *Patella*, above all other fo However, the type of food to which they were accustomed was also important and, once feeding commenced on a given type of food, it was often necessary to accustom them to a new food (by fee the new food mixed with the original food). The preference for chopped food became so habitual they did not take their naturally occurring food, such as live copepods and other crustacea, when it offered to them. It is probable though that this food would have been taken if enough had been avail and the trials carried out for some time, or if the fish had originally been induced to feed on this f

Behaviour During Feeding

Food was usually presented to the herring at one point only, the centre of the tank. It was scatte on the water surface and taken by the fish as it sank to the bottom. The herring were never seen to food from the bottom of the tank.

Before feeding the herring usually swam slowly about the tank in a loose shoal. After the doors lifted and food added the herring formed a tighter shoal. Shoaling persisted for a variable length of until feeding commenced, this time being called the "refractory period". The length of the "refrac period" was roughly inversely proportional to the general feeding activity of the fish. This was class into four groups based on the general activity of the fish and the amount of food reaching the bott These four groups with the appropriate "refractory periods" are shown below:—

Active (A)	—	5–15 secs., mean 10 secs.
Less active (<A)	—	7–35 secs., mean 15 secs.
Moderate (M) Poor (P)	—	7–75 secs., mean 40 secs.

At the end of the refractory period the herring broke shoal formation and started to feed. They not usually feed when shoaling. This might have been due to a fright reaction, the overt indicatio

was the formation of a shoal. Shoaling, however, is not necessarily the result of a fright reaction; obable that herring normally aggregate and swim in shoals. Observations on the feeding behaviour vidual fish suggest that they would be unable to orientate themselves in relation to other fish when act of taking food. Thus feeding in the sea will probably not occur when the fish are in shoals less of whether these shoals are the result of a fright stimulus or whether they are a normal means gression. If herring break their shoals when feeding and reform them when no more food is available, ill tend to aggregate in areas where food is to be found.

e herring actively searched for their food, depending as far as could be judged entirely on visual for its location. The fish either swam rapidly toward a food particle, taking it with a definite , or glided towards it taking it with a smooth "sucking" action. The fish usually took the food from and then immediately made a sudden turn and swam rapidly away. Sometimes the fish took more ne piece of food at a time, but they usually swam round before feeding again.

he particle was large the herring seized it, usually from below and proceeded to shake it violently sting and turning. The food might be released and recaptured many times before it was finally wed. If the piece taken into the mouth was very large the fish appeared agitated, swimming in jerks and convulsing the body until the piece was eventually ejected from the mouth. On two ns it was observed that a piece was rejected, after much rapid movement, by way of the opercular g, the operculum itself being held widely open and the gill bars wide apart.

ere was no sign of fierce physical competition during feeding in aquaria where the food supply lequate. If two fish approached the same piece of food one or other veered away. However, the fish generally took more food.

e feeding behaviour of the herring in these experiments confirms the deduction of Hardy (1924) erring feed by a definite act of capture. This has been also observed in aquaria by Battle *et al* (1936), n (1939), Bückmann *et al* (1953) and Verheijen (1953). The normal food of herring consists partly ve organisms which could only be taken by a definite act of capture.

rring have not been seen to take food from the bottom either in these experiments or in those of us workers. An examination of the morphology of the herring head shows that the lower jaw pro- beyond the upper jaw which would make feeding on the bottom very difficult. There are many s, however, of herring stomachs containing herring eggs. While these eggs usually develop on the n, it is likely that they are taken by the fish during the spawning act or when floating after being ed from the bottom.

TITY OF FOOD CONSUMED

e herring, which varied in number (see Table I), were fed each day with a weighed amount of food. were usually offered about 25 g of food four times a day making a total of about 100 g per day or 5 g per fish. Any food falling to the bottom was removed and weighed and in this way the food over a period of some months was recorded (see Table I).

e maximum amount of food taken at any one feed was 115 g of chopped squid by 22 herring, ut 5 g per fish. Previously the fish had undergone a 16 hour (overnight) period during which they ot fed and on the preceding day 100 g of food had been given in four separate feeds. This weight l (115 g) was exceptional for a single feed though the fish quite often took 4–5 g in the course ay.

ne measurements were made on the volume of herring stomachs by filling dissected stomachs acity (without distension) with a graduated pipette. The volumes ranged from 1·2 c.c for fish of n to 1·6 c.c for fish of 30 cm. We may take a figure of 1·2 c.c for these experimental herring which that fish can take in about 1·4 g of squid without distending the stomach. The average daily intake 3 g which would mean emptying the stomach twice per day (see section on passage of food through t). The fact that 22 herring each consumed over 5 g in one feed must mean that the stomach was istended or that food passed straight through it.

urther consideration of the effects of feeding on the growth of herring is contained in the discussion.

TABLE I

Period	Food consumed (g)	No. fish	Average Temperature (°C)	Mean Consumption /fish/day (g)
10.1.57-31.1.57	1,264	24	11·13	2·4
1.2.57-28.2.57	1,704	24	11·00	2·5
1.3.57-31.3.57	2,732	24	11·21	3·7
1.4.57-30.4.57	1,725	24	10·86	2·4
1.5.57-31.5.57	2,128	24	12·46	2·8
1.6.57-30.6.57	1,821	24	13·29	2·5
1.7.57-31.7.57	2,340	22	14·17	3·4
1.8.57-31.8.57	1,819	22	14·07	2·7
1.9.57-30.9.57	1,750	22	11·35	2·7
No. Days	Total food consumed (g)	Mean No. fish	Average Temperature (°C)	Mean Consumption /fish/day (g)
264	17,283	23·33	12·17	2·8

Selection of Food

This may be divided into primary selection, before the food has entered the mouth, and second selection after the food has entered the mouth.

1. *The Effect of Size and Shape of Food on Selection*

A sheet of squid muscle 4 mm in thickness was cut into different shapes and sizes and fed to herring. The results are given in Table II.

TABLE II

Dimensions		No. of pieces presented	No. taken
Rectangles	15·0×0·3 cm	2	2
	9·0×0·3 cm	1	1
	7·0×0·5 cm	5	2
	5·0×0·5 cm	5	4
	3·0×0·5 cm	5	5
Squares	1·5×1·5 cm	5	0
	1·0×1·0 cm	5	0
	0·5×0·5 cm	5	5
Triangles	1·0 cm sides	5	0
	0·5 cm sides	5	5
Circles	1·5 cm diam.	5	0
	1·0 cm diam.	5	0

The limiting factor in these experiments appeared to be the width of the food rather than its sh or length. If the food was 1·0 cm wide or wider, the fish did not take it. The width of the herring's m when fully distended is somewhat less than 1·0 cm.

The herring took very long thin pieces of food, up to 15 cm, and the end of these sometimes proje from the mouth for 10–15 minutes afterwards. As herring will take sand eels and occasionally sm gadoids at sea this is not a surprising result.

2. *The Influence of Colour of Food on Selection*

Pieces of squid were dyed with red, blue and green commercial icing sugar dyes. In a considera number of experiments, different combinations of colours were fed to the fish, with, and without, untrea white squid. In no case was preference shown for a particular colour and the fish took all colour readily as untreated squid.

another experiment rectangular coloured strips of food 0·3 cm wide and varying in length from 5·0 cm were fed to herring. Again no preference was shown for any particular colour.

seemed that the herring would attempt to feed on anything presented to them. They tried, for ce, to feed on bits of mussel shell, on the thermostat tube, on the bulb of a thermometer placed in ater and on pieces of rust. Thus primary selection of food seemed to be purely visual, the fish taking ing that could be accommodated in the mouth, regardless of its colour, shape or chemical nature, rying to take objects which were too large. There seemed to be little chemotactic influence in ry selection as mussel extract poured into the water had no effect on them nor did two muslin uspended in the water, one containing chopped mussel and the other a stone.

ter taking the food into the mouth, secondary selection took place, the fish rejecting practically hing except the food to which they were accustomed.

he Influence of Texture and "Taste" of Food on Selection

hile texture and "taste" were not involved in primary selection, they were both important in lary selection.

erring were fed with small pieces of compressed cotton wool (resembling chopped squid in colour, id to some extent shape), soaked in various substances as follows:—

tton wool soaked in tap water

" " " " squid extract (prepared from washings of finely minced squid)

" " " " human saliva

" " " " sucrose solution

ie herring took such pieces of cotton wool into the mouth and then immediately rejected them lless of the four treatments used. Feeding soon fell off to a low level of intensity with cotton wool came normal when squid was given again. If a mixture of squid and cotton wool pieces soaked in extract was fed after feeding with cotton wool alone, a visual selection took place, the herring mainly the squid and very little of the cotton wool.

ese results indicate the apparent importance of texture in selection. It was also noticed in various g trials that herring took more readily to squid, limpet, mussel and liver, all of rather similar e, than they took to other substances such as yeast, fish meal and other foods which were both ially prepared and less smooth in texture.

first it seemed that chemo-reception played a less important part in secondary selection. Herring , for instance, take putrifying mussel as readily as fresh mussel. The importance of taste was tested ating squid in various ways, as shown in Table III.

TABLE III

Food	Treatment	Percentage food taken
Squid	Untreated	100
"	Boiled for 1 hour	25
"	Boiled for 2 hours	0
"	Kept in refrigerator for 24 hours	100
"	Siphoned from bottom of aquarium after 24 hours	0
"	Washed in running water for 1 hour	c 90
"	" " " " " 2 hours	c 90
"	" " " " " 3 hours	60
"	" " " " " 4 hours	40
"	" " " " " 5 hours	33
"	" " " " " 6 hours	c 25
"	" " " " " 7 hours	c 20
"	" " " " " 24 hours	0
"	" " " " " 24 hours and soaked in squid extract for 1 hour	100
"	Extracted with ether for 1 hour	100
"	" " " " 4½ hours	90
"	" " " " 8 hours	100
"	" " " " 24 hours	100
Gelatine	15% gelatine made up with squid extract	100
"	15% gelatine made up with milk	0

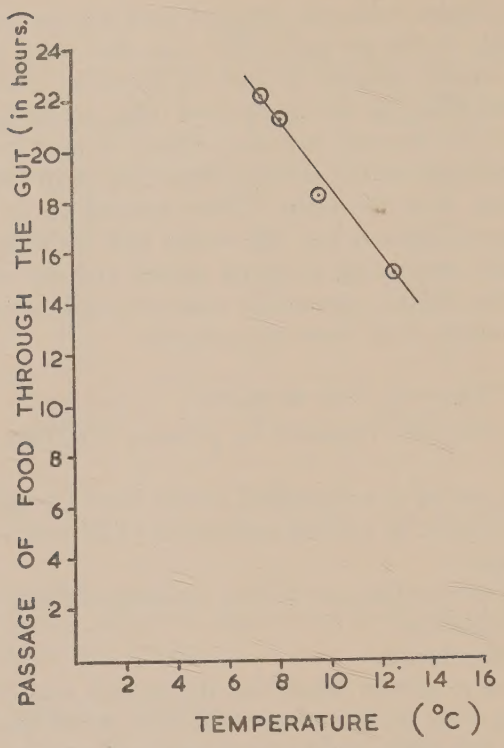

Fig. 1 Showing the time taken for food to pass through the gut at different temperatures.

These results show quite clearly that squid which has had water-soluble, but not fat-soluble, substan leached out, was no longer palatable to herring. This suggests that the taste of water-soluble amino a and/or carbohydrates was of importance in selection. The critical time for leaching appeared to be th to four hours. At this stage the specific gravity of the squid became noticeably reduced and the pie remained at the surface or sank very slowly. In particular, the use of gelatine cubes made up with sq extract or milk showed the importance of taste as they were identical in shape and colour and sim in texture to squid. Gelatine cubes could provide a very useful means of introducing desirable fo constituents which they will not normally take into the diet of fish, the taste of these constituents bei masked by squid extract.

Observations on the herring in these experiments showed that they rejected material of unsuita texture immediately, but that food of unsuitable taste was only rejected after a few seconds had elaps

Regarding other clupeoids, it has been shown (Anon, 1952) that chemoreception plays an importa part in primary selection of food by the sardine, *Sardinops caerulea*. Vilter (1950), however, describi the retina of the sardine (*Sardina pilchardus*) shows a very high cone: rod ratio (8:1) in the ventral regi of the eye and relates this to the habit of this fish of feeding selectively on planktonic organisms. T indicates that detection and primary selection of food is normally visual. Brett (1957) states that t lenses of the eyes of clupeoids are situated so as to give the widest field of vision, particularly above t fish. This is the region in which the herring usually detects its food (see section on feeding behaviou

It is interesting to note the correlation between selection of food by herring, namely a primary vis detection and selection and a secondary chemotactic and textural selection, with its brain structu This is reviewed in an appendix to this paper.

Effect of Low Temperature on Feeding

The effects of low temperatures on feeding are shown in Table IV. The observations were ma when there was no temperature control during the months of January and February. Light measureme were not made, but during the course of the observations the days were dull and the sky overcast.

TABLE IV

Water temperature (°C)	Feeding activity
2·0	No feeding, fish inactive at bottom of tank
2·5	" " "
3·0	" " "
3·8	" " "
4·0	Feeding moderate, fish "sluggish"
4·5	Feeding moderate, fish "lively"
4·8	Feeding active, fish "lively"
5·9	Feeding active, fish "lively"

here appeared to be a critical low level of temperature of 4·0°C; below which feeding did not occur. : low temperatures were not maintained for any length of time and the fish were not necessarily natised to them. Johnson (1939) found that herring would not feed at temperatures below 4°C and was no question of the fish being acclimatised in his experiments. Battle *et al* (1936) and Farrin *et al*) both found that herring kept in aquaria at low temperatures for some time would feed at tem- ures as low as 1°C.

E OF PASSAGE OF FOOD THROUGH THE GUT

llowing Maltzan's (1935) method with carp, measurements were made by feeding herring with red squid interspersed with normal squid. The time for digestion was found from the time difference en feeding with coloured squid and the appearance of coloured faeces in the tank.

was observed that the process of feeding acted as a stimulus for defaecation and that differing nts of food offered before and after giving coloured food considerably altered the rate of passage d through the gut. This is shown in Table V.

TABLE V

Amount of feeding before giving coloured food	Amount of feeding after giving coloured food	Average temp. (°C)	Time, in hours, for coloured food to pass through gut	
			Shortest	Longest
Starved for preceding 48 hours	Fed a total of 4 g/fish over following 6 hour period	14·3	8	>31
Starved for preceding 48 hours	Starved for following 24 hours and fed a total of about 4 g/fish during following 3 hours	12·3	24	48
Starved for preceding 24 hours	Fed a total of 4 g/fish over following 6 hour period	12·3	8	>24
Fed a total of 4 g/fish over preceding 8 hour period	Starved for following 24 hour period	12·0	<16	>40
Fed a total of 4 g/fish over preceding 8 hour period	Starved for following 16 hours then fed a total of 4 g/fish over next 6 hour period	12·6	<15	>24

ius food took longest to pass through the gut (i.e. 24 hours at 12·3°C) when the fish were starved before and after the test feed. Feeding before the test feed (compare Expts. 2 and 4) and feeding the test feed (compare Expts. 1 and 2) both accelerated the passage of food through the gut. The of starvation before the test feed did not seem to matter (Expts. 1 and 3). The amount of feeding he test feed might affect the maximum time taken for food to pass through the gut (Expts. 4 and 5). order to test the effect of temperature on the passage of food through the gut, experiments were

carried out at different temperatures using the following technique. The fish were fed at an averag
4 g/fish during the 8 hours before the test feed. This was then administered and the fish starved fo
hours. They were then again fed at a rate of 4 g/fish for the next 6 hours. The results are shown in Fig
There appeared to be a linear relationship between temperature and passage of food through the
within the range 7·5–12·5°C, the time varying from 15-23 hours. The Q10 over this range was 2·

Effect of Light on Feeding

1. *Variations in Light Intensity from Day to Day*

It was observed that feeding intensity fell off on bright days. Daily measurements of light inter
in metre candles, were therefore made when the fish were first fed. At the same time a visual estim
of feeding intensity and activity was made using the categories active (A), less active (<A), mode
(M) and poor (P).

Extracts from the daily record book shown below indicate the inhibiting effect of bright days
feeding.

Date	Temp.	Food	Light intensity (m.c)	Feeding activity
26.6.57	12·0	Chopped squid	9,100	<A
27.6.57	12·5	,, ,,	700	A
28.6.57	13·4	,, ,,	2,300	A
29.6.57	14·5	,, ,,	>38,000	P
30.6.57		No feed		
1.7.57	16·0	Chopped squid	9.500	A
2.7.57	15·5	,, ,,	26,600	<A
3.7.57	15·8	,, ,,	3,800	A
4.7.57	15·3	,, ,,	3,600	A
5.7.57	15·5	,, ,, and limpet	21,300	<A
6.7.57	14·9	Chopped squid	4,600	A
7.7.57	14·8	,, ,,	28,100	<A
8.7.57	15·1	,, ,,	19.000	M

The average light intensities over a period of five months for each feeding category are given below

Active	A	—	3,200 m.c	(On 75 days)
Less Active	<A	—	14,100 m.c	,, 47 ,,
Moderate	M	—	14,400 m.c	,, 18 ,,
Poor	P	—	31,200 m.c	,, 8 ,,

In view of the apparent importance of light in feeding a series of experiments were carried out un
controlled conditions to determine the optimum light intensity for feeding.

2. *Low Light Intensities*

The different light intensities used in the experiments were obtained from tungsten filament bulbs
different wattage controlled by a rheostat or Variac transformer. Measurements of light intensity we
made above the surface immediately below the light with an Eel photometer. The experiments we
carried out during the day and daylight was excluded from the tank by black curtains. The temperatu
was maintained at 11°C.

The following procedure was adopted for each light intensity. The light intensity was maintained
the required level for three hours before feeding; forty pieces of squid were then introduced into the tan

umber reaching the bottom being used as a criterion for measuring feeding intensity. The food ıtroduced from the outside to a point just above the surface and immediately below the light by ber tube. A method of washing the food through the tube with sea water was standardised and on each occasion.

ıe quantity of food taken at different light intensities by 22 fish is shown in Tables VI, VIII and .

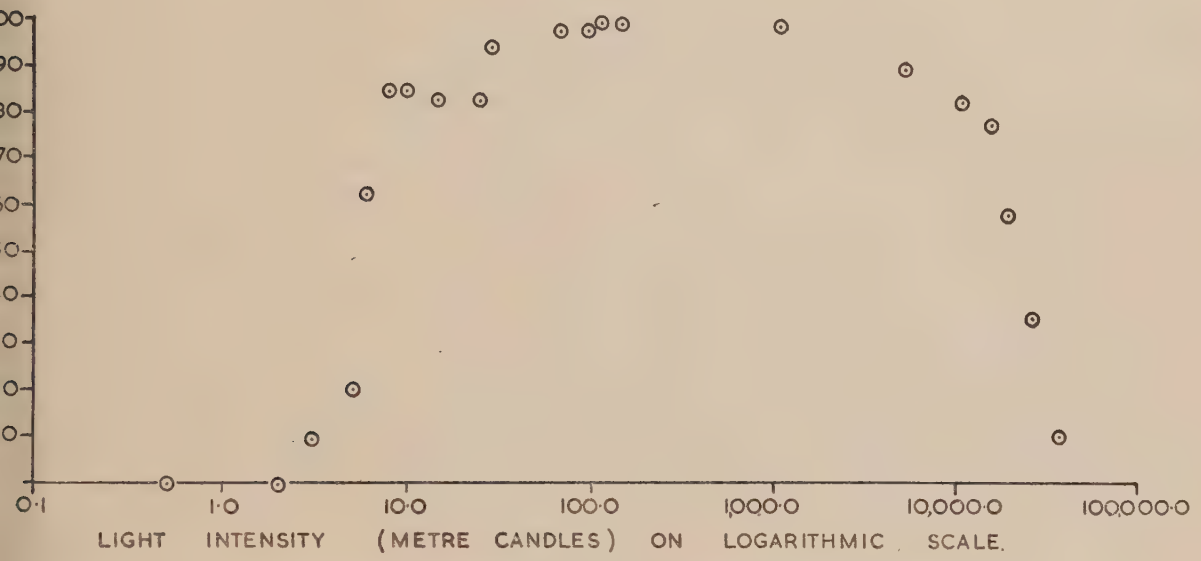

Fig. 2 Showing the amount of food taken at different light intensities.

TABLE VI

Intensity (metre candles)	Quantity of food presented (pieces)	Quantity taken (pieces)	Percentage taken
0·0	40	0	0
0·5	40	0	0
2·0	40	0	0
3·0	40	4	10
5·0	40	8	20
6·0	40	25	63
8·0	39	33	85
10·0	40	34	85
15·0	40	33	83
25·0	40	33	83
30·0	40	38	95
70·0	40	39	98
100·0	40	39	98
110·0	40	40	100
150·0	40	40	100
1,100·0	40	40	100

ere appeared to be a critical lower light intensity below which no feeding occurred. Above this ; intensity increased to a maximum at about 110 m.c. The critical lower light intensity of 3·0 m.c gher than the maximum to be expected from moonlight which is about 0·25 m.c according to ı (1929). Johnson (1939) has shown that herring will feed in moonlight.

experiment was therefore carried out in which the herring were acclimatised to moonlight (full ıt about 45°) for about two hours, and were then fed in the usual way, as shown in Table VII.

The fish took the blue and red squid more readily than the white squid. The reason why the herri fed in full moonlight (0·25 m.c), which is a lower light intensity than the minimum found in the previ experiment (3·0 m.c), is not clear. The quality of the light may be responsible, as the light produ from a tungsten filament lamp working at low voltage contains more light of long wavelength thar found in moonlight. The herring would not feed in the dark or in moonlight when the moon was full so it seems that 0·25 m.c is the minimum light intensity for feeding.

TABLE VII

Type of food	Quantity of food presented in moonlight (pieces)	Quantity of food eaten (pieces)	Percentage eaten
Normal squid (white)	50	8	16
Squid dyed blue	50	19	38
Squid dyed red	20	4	20

3. *High Light Intensities*

Further experiments were then carried out using high light intensities. The conditions were the sa as for earlier experiments at low light intensities except that bulbs of 1000 and 1500 watts were used give intensities of up to 27000 m.c. For intensities greater than this the fish were fed in bright sunli with the covers removed from the tank. The results are given in Table VIII and Fig. 2.

TABLE VIII

Intensity (m.c)	Quantity of food presented (pieces)	Quantity of food taken (pieces)	Percentage taken
5,600	40	36	90
10,900	40	33	83
16,300	40	31	78
19,500	40	23	58
27,200	40	14	35
>38,000	60	6	10

In the case of the last two observations control experiments were carried out. Immediately af feeding at the high light intensity the fish were fed at a lower intensity by shielding the light source (Table IX).

TABLE IX

Intensity (m.c)	Quantity of food presented (pieces)	Quantity of food taken (pieces)	Percentage taken
27,200	40	14	35
150	40	38	95
>38,000	60	6	10
114	40	21	53

During and immediately after feeding at the highest intensity the herring appeared much disturb swimming rapidly near the bottom of the tank. The return to normal feeding activity took longer af this experiment than any other.

seems from Fig. 2 that there was an optimum zone of light intensity ranging from about 100 to m.c (using artificial lights). It was also found that daily feeding was most active when the light ity (due to the sun) was low, the average for the active feeding category (A) being about 3000 m.c.

iurnal Feeding Rhythm

was decided to ascertain whether there was a diurnal feeding rhythm under aquarium conditions. experiments were carried out, each starting at a different time of day. In each experiment 22 fish offered hourly a total of 20 g of squid. After each feed the uneaten food was siphoned off and weighed. s way the amount of food taken each hour by these fish was estimated.

uring the dark hours, with no moon, the fish would not feed at all (see section on feeding at low ntensities), unless artificial light was supplied. A 15 watt bulb was therefore suspended 25 cm he surface of the water and this was switched on 2-3 minutes before feeding and switched off again n as the uneaten food had been siphoned off.

e first experiment was started at 09·00 hours, the fish being fed every hour until 17·00 hours. l of 150 g was taken, the feeding intensity being high during the whole day.

e results for the other three experiments are shown in Fig. 3. The first was started at 18·00 hours e fish fed every hour until 17·00 hours the next day. In the second, feeding was started at 23·00 one day and continued until 12·00 hours the next day. In the third, feeding was started at 04·00 one day and continued until 17·00 hours the same day.

ere appeared to be signs of a diurnal feeding rhythm, a decrease in feeding intensity occurring the hours before dawn (04·00–08·00 hours). This did not appear to be due to the fish becoming d or to a cycle of digestion, as it occurred regardless of the time feeding was started. The fairly tensity of feeding found during the daylight hours towards the end of each experiment was prob- ue to the fish being satiated.

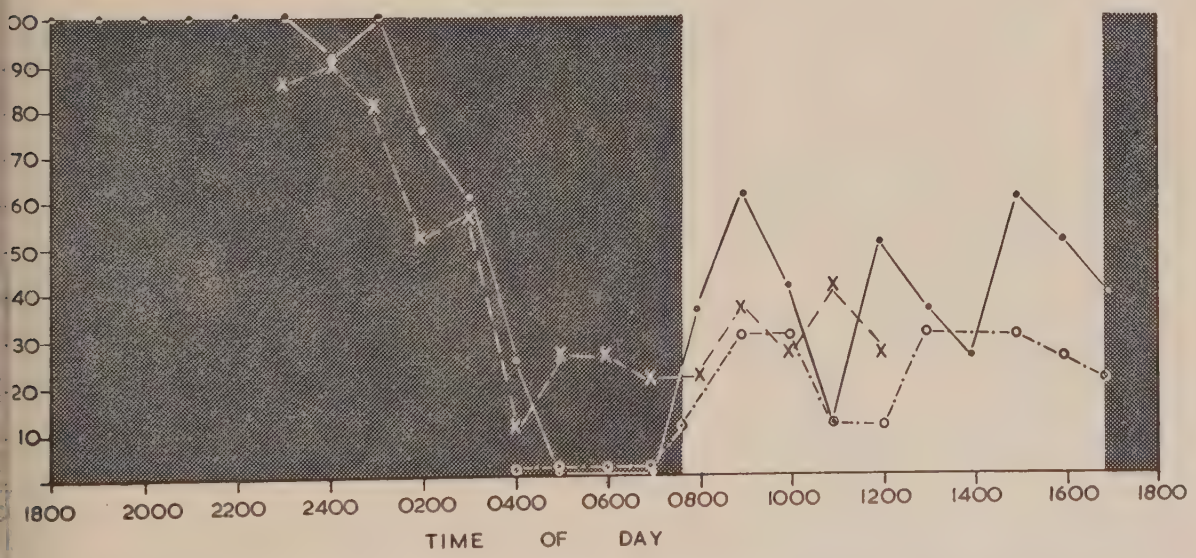

Fig. 3 Showing the amount of food taken at different times of the day and night.

t of Noise on Feeding

violent disturbance or noise around the tank during the course of feeding resulted in its cessation e formation of a shoal.

effect of sound waves of different frequencies on feeding behaviour was therefore determined

by a variable frequency sound unit. The loudspeaker, in a watertight housing, was placed in mid w in the tank and directed towards the position where the herring fed, this being about 0·5 metres a Food was placed in the tank and after feeding had commenced the unit was switched on at the de frequency, the amplitude being kept constant. In a later experiment the loudspeaker was placed a the surface. The results are shown in Table X.

TABLE X

Position of loudspeaker	Frequency (c/s)	Response
Below surface	30,000	No response
,,	15,000	No response
,,	10,000	No response
,,	5,000	Slight "startle" reaction when sound started but no effect on feeding
,,	1,000	Slight "startle" reaction when sound started but no effect on feeding
,,	500	Slight "startle" reaction when sound started but no effect on feeding
,,	100	Reacted strongly when sound *started* or *stopped*—feeding stopped and the fish forme shoal. If sound was left on or off feeding started again.
,,	75	
,,	50	
,,	10	
Above surface	30,000-1,000	No response
,,	500	Slight "startle" reaction when sound started but no effect on feeding
,,	100	Reacted strongly, particularly when sound *started*. If sound was left on they retur to feed
,,	75	
,,	50	
,,	10	

The sound in the experiments was mainly in the form of a sine wave. No differences in beha were observed when a square wave was used. While the sound was usually continuous, no differenc behaviour were observed when the sound was pulsed.

Another experiment was carried out with an Atlas (30 kc/s) portable echosounder. The transn was placed in the water near the feeding point. During feeding the sounder was switched on. The he showed an immediate flight reaction but returned to feed after about 30 seconds. After repeating t number of times the herring became used to the sound and continued to feed when it was switche When the transmitter was out of the water no reactions were observed when switching on. This e sounder made an audible ticking noise of low frequency, as well as producing a pulse of 30 kc/s, a seemed likely that the herring were responding to the former. The fact that herring were not adve affected by high frequency noises (though they might have been audible), and were only tempo affected by low frequency noises, is important. It suggests that the behaviour of herring will no affected for more than a short period by commercial echosounders (which have a high frequency p of 10 kc/s or more, and also a low frequency component). This has also been shown by Dow an Skoglund (quoted by Moulton and Backhus 1955) and by Verheijen (1953) and repeatedly by research vessels.

Another experiment was carried out to test whether herring make any noise when feeding. A hy phone was placed in the tank but no noises were heard which could be attributed to the fish.

Effect of Tagging on Behaviour

As a separate experiment approximately half the herring were tagged with various tag type different positions on the body. During this process the fish were handled for 10–15 seconds and sl wounds were made as the tags were inserted. After tagging the fish stopped feeding for periods ran from 48–72 hours. However these and earlier experiments (see Wood, Parrish and McPherson 1 showed that tagged fish fed, manoeuvred and shoaled normally and that they were not attacke avoided by other fish. Tag shedding rarely resulted in death.

Tagging is now used widely in herring research to investigate migrations and these results ar interest as they show that tagging need not interfere with the normal behaviour of the fish.

LEX FACTORS IN FEEDING BEHAVIOUR

rring 17–20 cm long were kept in tanks of two different sizes for about 10 weeks and food was l daily. In the larger tank (7,500 litres) two fish commenced feeding during the first week after e and others soon followed suit. In the smaller tank (750 litres) no feeding was observed over the 10 week period. At first the temperature in this small tank was the same as the large one (about but it gradually declined to about 7·5°C. In no instance did it go as low as the critical temperature .

e fish in the small tank became thin and the fat reserves depleted or lost. They were then trans- to a tank holding 3,000 litres but they still did not feed. Finally eight surviving fish (having been l for 10 weeks) were transferred to the tank holding 7,500 litres where other fish were actively g. One hour afterwards at least two of the transferred fish were feeding and during the next three he remainder started feeding.

re both space and community effect were important. Herring, when confined in tanks which were all, did not feed even after failing to take food for ten weeks. Under these conditions they were not ated by the presence of feeding fish 10–12 cm long. In a tank of adequate size the presence of g fish accelerated the initiation of feeding in non-feeding fish. In such tanks, however, feeding eventually be initiated in the absence of feeding fish.

aller herring, 10–12 cm long, could be induced to feed in tanks of 750 litres. When feeding, they t appear to accelerate the initiation of feeding in non-feeding larger fish (17–20 cm), even in large itre tanks.

DISCUSSION

INTAKE

e average amount of food taken per fish per day was 2·8 g between 10th January 1957 and 30th nber 1957. Four feeds were made each day (except on Saturday, when one only was given and nday when there was no feeding). As some food was almost invariably not taken this represents ximum average intake using this type of feeding. Although some apparatus for continuous feeding ed it never worked satisfactorily. Is this figure of 2·8 g below the average daily intake at sea under eding conditions?

is is suggested by observations on the maximum feeding rates, i.e. in *one feed* 22 herring took 115 g ped squid or 5·23 g each, equivalent to just over 4 c.c of squid. Observations made on fish caught showed that the stomach of a particular fish contained four *Gadus esmarkii* all measuring about ng and occupying a total volume of 4 c.c. The volume of the herring stomachs measured in these nents was 1–2 c.c. undistended. Thus considerable distension must take place before the stomach ke two or three times its normal volume.

s of interest to consider how the figures of average feeding rate can be correlated with the rate of of food through the gut. Battle *et al* (1936) working with herring 14–16 cm long found that n of copepods varied from 25½ hours at 6°C to 6–7 hours at 20°C. At 11–12°C it was about 15 In older fish the gut cleared more rapidly. Results here, with fish of about 20 cm, indicate that the l amount of feeding considerably affected the rate of passage of food through the gut and that at od would pass through in 8 hours. It seems reasonable to assume that at 11–12°C the gut may be nd emptied twice in 24 hours, when the food is taken in small quantities of about 1 g at a time. ood is bulky (as when feeding on small fish), and taken in large weights up to 4 or 5 g it is likely at least 24 hours to pass through the gut. It therefore seems that the daily intake of herring at nlikely to exceed 4 to 5 g at the most and may well be less. Savage (1931) working on the North rring found that the average volume of the stomach contents varied from about 1 c.c per fish in ril to 0·2 c.c per fish in September though a few stomachs contained 3–4 c.c. Reports of herring g themselves are quite common however (for instance Lucas, 1936). Unpublished data on feeding ing off the Scottish East Coast show that the stomachs may sometimes contain up to 5 g of food *lytes*) but more often 1–2g. Jespersen (1932) showed that the stomach contents of Icelandic herring occupy as much as 10 c.c.

Thus the average weight of food taken by these aquarium herring (i.e. 2·8 g/fish/day—equiv to about 2·3 c.c), ignoring the results for Icelandic herring, would not appear to be much less tha average taken at sea and might in some cases be much more.

These comparisons are only valid if the composition of the artificial food is similar to that of plan Herring have been fed mainly on squid. Work by Chen and Tuanmu (1946), De Gouveia and De Go (1951) and Inoue and Tanikawa (1952) show that the dry weight of squid muscle is about 23%. Pr comprises 12–19% of the wet weight, fat 1–2%, and ash 1–2%. The carbohydrate value is very being about 0·2%. Vitamin 'C' is also present. The data of Marshall, Nicholls and Orr (1934), Riley (1 and Vinogradov (1953) show that the dry weight of *Calanus finmarchicus* (a very important food orga for the herring) is about 15%. Protein comprises 10%, fat 4% and exoskeleton 1% of the wet weig

That squid is at least a partially satisfactory food is shown by both growth and maturation in t herring. The larger ones have shown signs of maturation up to stage VI though the smaller one still immature or in early stages of maturity.

It has only been possible to gauge growth by indirect means as the fish are not able to withs frequent removals from the tank. The average increase in length would appear to be 2–3 cm an weight 20–30 g over a period of 9 months. One small fish, however, must have grown from about 1 18 cm in that time.

It is interesting to consider the amount of food required for maintenance in other fish. Hatha (1927) showed the importance of size and temperature in the feeding of fish. Dawes (1930) using pl *Pleuronectes platessa*, fed with chopped *Mytilus*, found that the maintenance level (where weight rema steady) in weight of food per unit weight of fish, decreased with increasing size of fish and also decre as the temperature was reduced. The maintenance level varied from 77–168 mg/g fish/week. Maxi growth was found when the fish were fed at a rate of 6 g/day. Brown (1946a, b), working in much detail on trout, *Salmo trutta*, found that the maintenance level varied with temperature and size o in the same way as plaice. It was about 100 mg/g fish/week of meat (22·5% dry weight) for trout weig 50 g at 12°C and about 60 mg/g fish/week for fish of 100 g or more. If similar data for plaice are extr from Dawes (Tables 12, 16, 33 and 38) the maintenance level at 12°C for 50 g fish is about 100 fish/week and for 100 g fish it is 80 mg/g fish/week.

The average amount of food taken by the herring in these experiments has varied from about 420 mg/g fish/week assuming that the fish varied in weight from 40 to 100 g. This is well above the m tenance level for trout and plaice under similar conditions. The question arises whether the mainte level in herring is similar to that in trout and plaice. This seems doubtful as both trout and plaice to be much less active animals, at least in aquaria. If the arbitrary figure of double the average m tenance level of trout and plaice is taken for herring it is interesting to see how this fits in with gr data. The 40 g herring (with a maintenance level taken at 200 mg/g fish/week) were getting a double the maintenance level while 100 g herring (with a maintenance level taken at 140 mg/g fish/w were getting only slightly more than the maintenance level.

Brown (1946a) has shown that trout need the equivalent of their maintenance ration per w for each gram of weight increase per week. Thus if they are to increase in weight by 5 g in one w they will require six times the maintenance ration during that week. If such results can be ap to herring the 40 g fish should increase in weight initially by about 1 g/week and as they put on we this amount will progressively drop. The larger fish will initially put on less weight (i.e. 60 g fish a 0·5 g/week) and fish of 100 g are likely to remain about the same weight.

Such predictions are borne out to some extent by the growth of fish in the tank. The smaller originally about 40 g in January, appear to have grown to about 60–70 g in September and the l fish from about 80 to 100 g. No fish seem to have increased to a length or weight which might have b expected had they remained in the sea (about 25 cm and 150 g), which suggests that the feeding l must be stepped up for larger fish. These generalisations are of course complicated by such factor the larger fish taking more food and any possible psychological factor operating between large and s fish, as shown by Brown (1946a).

While the estimate of double the maintenance levels in plaice and trout seems applicable to her in aquaria, this does not seem to be so for herring at sea. Maturing fish at sea will increase in we

bout 60 g in January to about 150 g in August-September, the average increase in weight being 2·5 g per week. If the maintenance level is taken as double that of trout or plaice, the fish will) take in about 6 g of food per day at first and about 10 g of food per day at the end. This seems nlikely and indicates that the arbitrary maintenance level suggested for herring in aquaria is plicable to fish at sea, possibly due to a difference in food, the pattern of feeding or the activity fish.

T OF LIGHT INTENSITY ON FEEDING AND DIURNAL MOVEMENTS OF HERRING IN THE SEA

general, studies on herring in the open sea show that they undergo a diurnal vertical migration. the day the fish are usually near the seabed or in mid-water and are distributed in discrete units may or may not be orientated (i.e. they may or may not be shoals). At dusk the fish rise to the and spread out. It is usually considered that the herring start feeding at this time. At dawn they ain usually reforming into groups.

e conclusions from these experiments which may be applicable to an analysis of this diurnal on are as follows:—

1. Primary selection of food was by visual means.
2. The lowest level of natural light intensity at which herring fed appeared to be about 0·25 m.c.
3. The optimum light intensity for feeding lay between 100 and 1000 m.c. (The light intensity at the surface on a dull day would be about 10,000 m.c.)
4. There appeared to be a diurnal feeding 'rhythm' (in aquaria), feeding intensity being reduced in the early morning.
5. Herring responded most to low frequency noises (below 100 c/s) though they were also sensitive to noises of at least 5,000 c/s.
6. Herring did not appear to feed when in shoals.

re is also some published work which is applicable to an analysis of the diurnal migration of . Lissner (1925) considered that herring fed most actively at dusk and ceased feeding after mid- espersen (1928) sampled young herring (6–15 cm) throughout 24 hours from December to March sh waters; he found that maximum feeding took place in the afternoon and evening (14·00–21·00 nd that feeding was at its lowest between 23·00 and 09·00 hours. Mužinić (1931) considered that in the autumn fed mainly during the afternoon and evening and again at 04·00 hours. Battle 936) and Johnson (1939) found that herring kept in aquaria could feed by moonlight but not in c. Vučetić (1955) suggested that the adult sardine, *Sardina pilchardus*, in the Adriatic from February ast fed mainly in the afternoon.

obvious difficulty in estimating these times of feeding is in deciding how long food has been in Rates of digestion vary with temperature, and with other factors such as the amount of feeding. n the experimental evidence described in this paper and from published work, it would seem rring feed mainly at dusk as they are rising to the surface. They would appear unable to feed at cept in bright moonlight, or unless some other factor is operating. For instance, the fish might be on phosphorescent organisms or on organisms producing noises of a frequency to which the are sensitive.

question arises as to whether fish also feed at other times. It seems unlikely that fish will feed the day if they are in shoals. On the other hand the compact groups of herring shown up by nders during daylight might not be shoals but groups of fish, which are not orientated, actively on a small patch of plankton or other food organisms. The optimum light intensity for feeding ia seems to be 100–1000 m.c. These conditions will be found in the sea during daylight at depths from 7–40 metres (using data for the light intensity and turbidity on the Scottish east coast grounds in 1957). The critical level for feeding, 0·25 m.c, will be found then at depths ranging -80 metres. Herring are frequently to be found at these depths during the day and it seems that ns might be ideal for feeding if the fish are not in shoals.

ther the fish feed at dawn is uncertain. The experimental work which has been described and ublished work indicate that they do not feed at dawn. There is no doubt, however, that frequent of stomach contents during a 24 hour period is not only very difficult, due to the need for getting

samples throughout such a period, but even if this can be done, there is the problem of deciding how food has been in the gut. In general, however, the evidence points to the period preceding dusk as the most important feeding period.

Several different stimuli may control the diurnal vertical movement. While the presence of food almost certainly important for modifying the movement, as are temperature gradients and other hydrographic factors, it seems likely that light is the dominant stimulus. Herring will, for instance, undergo a diurnal migration even when not feeding (Richardson 1952). The herring are then probably remaining in an optimum light intensity, rising within it to the surface at night and sinking again at dawn. When the light fails to the extent that the herring are unable to remain within their optimum, there still remains no reason why they should descend into regions which can only be regarded as even darker. Moreover they may be positively stimulated to stay at the level to which they are adapted from the point of view of hydrostatic pressure. Thus they would make random movements about this level, but would not make movements which would demand further adaptive changes in the swim bladder system. At dawn the dominant light stimulus would again control the movements of the fish.

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SUMMARY

1. Observations on the feeding behaviour of herring (16–22 cm in length) have been made in an aquarium.

2. The herring, after being established, preferred chopped *Loligo*, *Mytilus* and *Patella* above all other foods, both natural and artificial.

3. The behaviour of herring during feeding is described.

4. The average weight of food taken per day over a period of nine months was 2·8 g. This amount is related to the growth and maturity of the herring, their possible maintenance requirements, and differences which might be expected with herring in their normal environment. The fish were found to have grown 2–3 cm and 20–30 g and some had reached maturity stage VI during a period of nine months.

5. Selection of food seemed to take place in two stages. There was a primary selection by eye regardless of size, shape or colour. Secondary selection was first tactile and then chemical, food of unsuitable consistency or taste being rejected.

6. It appeared that the herring would not feed below a critical temperature of 4°C.

7. The rate of passage of food through the gut was measured. This varied from 8–24 hours, depending on temperature and the amount of feeding before and after the test feed. The Q_{10} over the range 12·5°C was 2·1.

8. Light intensity had a marked effect on feeding. No feeding took place at intensities below 0·25 m.c. candles (full moonlight) which is probably the threshold for feeding. Using artificial light, feeding gradually increased in light intensities from 3–100 m.c, the optimum for feeding being 100–1000 m.c. Between 1,000 and 5,000 m.c feeding gradually decreased and reached a low level at about 30,000 m.c.

:re appeared to be signs of a diurnal feeding rhythm such that feeding was reduced in the four)efore dawn.

ses with frequencies below 100 c/s caused a fright reaction and temporarily stopped the herring eding. Noises with frequencies above 100 c/s, including the high frequency pulse from a 30 kc/s nder, had no such effect though the herring responded to frequencies of at least 5,000 c/s. No were heard when a hydrophone was used during feeding.

herring did not feed for 48–72 hours after tagging. Tagged fish fed, shoaled and manoeuvred ly and did not affect the behaviour of untagged fish.

effect of space and social factors are mentioned.

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APPENDIX

THE BRAIN STRUCTURE OF THE HERRING IN RELATION TO ITS FEEDING HABITS

DUCTION

idence has previously been given of the importance of sight in the feeding habits of the herring. perception and selection of the food particle depended, as far as could be judged, entirely on visual i. A secondary selection process based first on the appreciation of texture and then on taste was when the food particle was within the buccal cavity. Evans (1952) states for fish in general that: ing is performed in a variety of ways which in turn finds its expression in the pattern of the brain. ross examination of the brain those senses most utilized by a particular species may be distinguished, is possible to infer, to some degree, the feeding habits of the species."

shows how the gross anatomy of the brain of four species of cyprinid fishes is closely related to eeding habits. The "mouth tasters" show relatively great development of the facial and vagal The "sight feeders" show the optic lobes as the predominant brain feature. In the "skin tasters" ial lobe shows the greatest degree of development.

is of interest to see whether the brain structure of the herring reflects the mode of feeding of the or this reason dissections and macro-sections of the brains of herring of different lengths and ities were made (see Fig. 4).

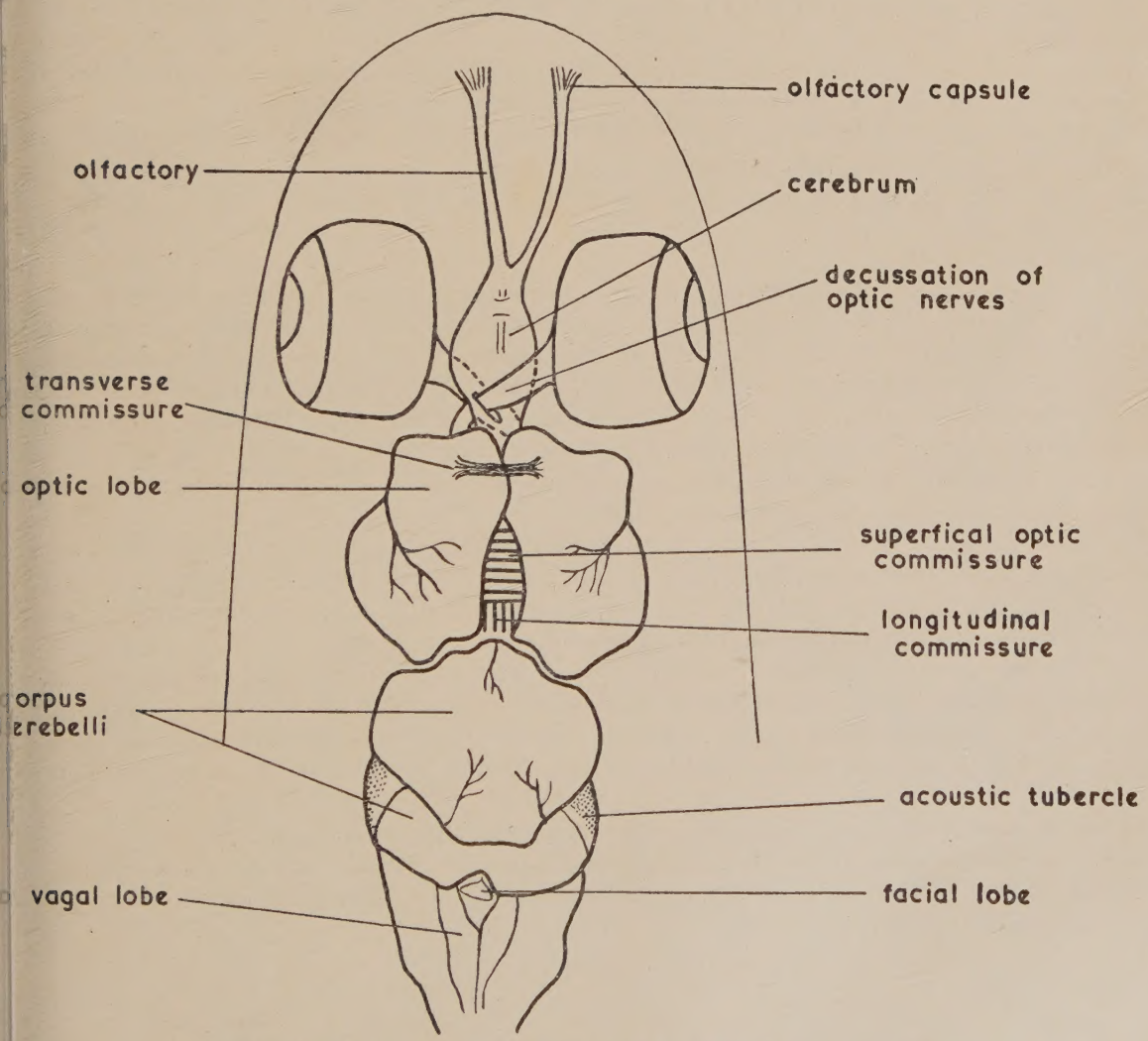

Fig. 4 Dorsal view of the herring's brain.

RESULTS

The fore-brain is small, lying between the eyes and is connected by fairly long olfactory tra the small olfactory capsule.

Immediately ventral to the fore-brain is the point of decussation of the optic nerves. The herr unusual among teleosts in that the nerve from the right eye passes through that from the left.

The optic lobes are very large, dominating the fore and mid brain. The two lobes appear dist separate externally, but on removing the roof of both lobes a large collection of nerve fibres is v linking right and left sides. This is the transverse commissure, and crosses immediately anterior t opening of the third ventricle.

There is also a more superficial commissure connecting the two optic lobes across the roof of th brain, immediately anterior to the cerebellum.

The raised floor of the optic lobes projects into each ventricle cavity.

Immediately posterior to the optic lobes is the large cerebellum. It overlies all of the mid and brain, covering most of the fourth ventricle. It does not encroach over the optic lobes.

Within the cerebellum are large columns of sensory and motor fibres running through the s column, via the spinal nerves, to the muscles of the trunk and tail.

Bi-lateral acoustic tubercles, situated in the ventro-lateral regions of the cerebellum receive se impulses from the ear and the lateral line. These areas are well marked in the herring.

The median corpus cerebelli lying between the acoustic tubercles receives sensory nerves fro body muscles.

A tract of fibres from the cerebellum, the longitudinal commissure, runs forward directly b and in part intermingling with, the fibres of the superficial optic commissure.

The "facial" lobe is exceedingly small in the herring and lies immediately posterior to the c cerebelli, projecting into the thin roof of the fourth ventricle.

The vagal lobes are also relatively small when compared with the other brain structures.

DISCUSSION

The large optic lobes of the herring's brain indicate the importance of sight in the feeding a of the fish. The presence of the commissures connecting the two lobes allows some degree of in exchange and co-ordination between the two lobes. Brett (1957) states that the arrangement lenses in the eye of the herring is such that a region immediately above the head (and presuma front and above too) is within the field of vision of the lenses of both eyes. This fact, taken in conju with the pattern of nerve fibres between the optic lobes and the ability of the herring to locate accu the position of swiftly moving food particles, suggests that there is at least some degree of bin vision in the regions above and in front of the fish.

The other dominant brain structure, the cerebellum, is the centre of co-ordination of motor acti The existence of tracts of nerve fibres from the optic lobes to the corpus cerebelli would allow t ordination between sensory optic impulses and motor muscular impulses necessary for the ex manoeuvrability involved during the capturing of the prey.

The acoustic tubercles receiving impulses from the lateral line and ear are well marked, as wou expected in the herring, possessing as it does a highly developed otolith system. The act of capturing swiftly moving organisms often results in rapid twisting movements in more than one plane a equilibrating function of the otolith would result in constant stimulation of the sensory nerves d feeding activity.

The facial lobe is small and indicates the lack of dermal chemoreceptors.

The vagal lobes are also relatively small and indicate that "mouth taste" is not the dominant r of selection during feeding. It would appear from feeding experiments that buccal selection is mo appreciation of texture than taste.

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